

A New Genus and Species of Facelinidae (Opisthobranchia: Aeolidacea) from the Caribbean Sea

by

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Abstract. A new aeolid species has been found throughout the Caribbean Sea. It possesses the characteristics of the family Facelinidae and the subfamily Favorininae, but its reproductive structures differ from those of all other genera. This species is therefore placed in a new genus and compared to other genera in the subfamily.

INTRODUCTION

The tropical western Atlantic opisthobranch fauna is incompletely known, and relatively depauperate compared to the Indo-Pacific fauna. Nevertheless, almost 300 species have been described. The warm-water western Atlantic opisthobranch species are primarily endemic, but there are also many ampho-Atlantic species (EDMUNDS, 1968, 1977; JENSEN & CLARK, 1983; ORTEA *et al.*, 1988; TEMPLADO *et al.*, 1991). A number of Caribbean-Panamic species are recognized, and are thought to be representatives of a shared Pliocene fauna (MARCUS & MARCUS, 1967; BERTSCH, 1979; GOSLINER & WILLAN, 1991). There are also circumtropical representatives, possibly remnants of the Tethys Sea fauna.

Eveline and Ernst Marcus provided a sound basis for further opisthobranch research, summarized in their checklist of western Atlantic warm-water opisthobranchs (MARCUS, 1977). Since then, several synonymies have been made and at least 26 new species have been added (CLARK & GOETZFRIED, 1976; EDMUNDS & JUST, 1983; GOSLINER, 1989; GOSLINER & ARMES, 1984; GOSLINER & GHISELIN, 1987; GOSLINER & KUZIRIAN, 1990; HAMANN & FARMER, 1988; MARCUS, 1980, 1983; MEYER, 1977; NUTTALL, 1989; ORTEA & TEMPLADO, 1989; TEMPLADO *et al.*, 1987; THOMPSON, 1977, 1980). This paper describes a new aeolid genus and species belonging to the family Facelinidae.

SYSTEMATIC TREATMENT

ORDER AEOLIDACEA

SUPERFAMILY CLEIOPROCTA

FAMILY FACELINIDAE

SUBFAMILY FAVORININAE

Genus *Pauleo* Millen & Hamann, gen. nov.

Generic diagnosis: Rhinophores smooth or weakly lamellate. Cerata arranged on pedunculate arches with one or two rows per arch. Foot corners tentacular. Anus cleio-proctic. Nephroproct interhepatic. Salivary glands simple. Oral glands absent. Jaw elongate, notched, and possessing a flange. Masticatory border with single row of denticles. Radula uniseriate with large, cuspidate rachidian teeth. Tooth shape triangular with many short denticles. Reproductive opening below anterior arch of first ceratal cluster. Reproductive system androdiaulic with proximal receptaculum seminis. Vas deferens non-prostatic. Penis with internal glands and proximal, non-glandular pouch containing vas deferens. Penial opening subterminal, unarmed.

Type species: *Pauleo jubatus* gen. & sp. nov., by original designation.

Pauleo jubatus Millen & Hamann, sp. nov.

(Figures 1–8)

Etymology: The numerous curly cerata that can bristle forward defensively suggested the generic and species names, which translate as “little lion’s mane.”

Material: Holotype: California Academy of Sciences CASIZ 077998, 1 specimen, 22 mm long. Specimen collected by J. Hamann on 24 May 1986; Grand Bahama, Bahamas, outer reef off Taino Beach (26°29'58"N, 78°36'45"W), at 20 m depth on a coral head on sandy substrate.

Paratypes: CASIZ 077294, 6 specimens, up to 28 mm long. Collected by T. Gosliner on 6 May 1991; S.W. Point, Grand Cayman, B.W.I., at 25 m depth on the gorgonian *Plexaurella dichotoma*.

United States National Museum of Natural History, USNM 860266, 1 specimen, 19 mm long. Specimen collected with the holotype.

Other collecting localities: Port Antonio, Jamaica, 2 specimens, largest 31 mm, at 13 m depth. Collected by J. Hamann, 23 August 1990. Discovery Bay, Jamaica, 10 specimens. Collected by J. Hamann on 14 December 1990, at 8 m depth, grazing on downed *Plexaurella dichotoma*.

Photographic records: Jackson Pt., Little Cayman, Cayman Islands. Photographed by Nancy Sefton, specimen on a coral head on a sandy bottom.

Bloody Bay, Little Cayman, photograph by Dr. Marc Chamberlain, November 1987, specimen on a patch reef at 10 m depth.

Lighthouse Reef, Belize, photograph by Thomas M. Sullivan, December 1984, of a specimen near the edge of a sandy reef at 12 m depth.

Eleuthera Island, Bahamas, photograph in COLIN (1978: 389), on a gorgonian at 20 m depth.

Guanaja, Honduras, 42 mm specimen photographed by J. Hamann, 8 August 1991, at 20 m on *Plexaurella*.

Systematic Description

External morphology: This translucent aeolid is suffused with pale orange on the head, tentacles, rhinophores, cerata, and dorsum. Underlying the orange suffusion is one of a variety of food-derived colors: orange, yellow, tan, pinkish beige, or blue gray. The animal has an elongate, slender, rounded body and a long trailing tail (Figure 1). A median, opaque white stripe extends along the head and down the full length of the body, narrowing between ceratal clusters. The line varies in width among specimens and may be interrupted. A small, opaque white crescentic patch is present on either side of the head just below the

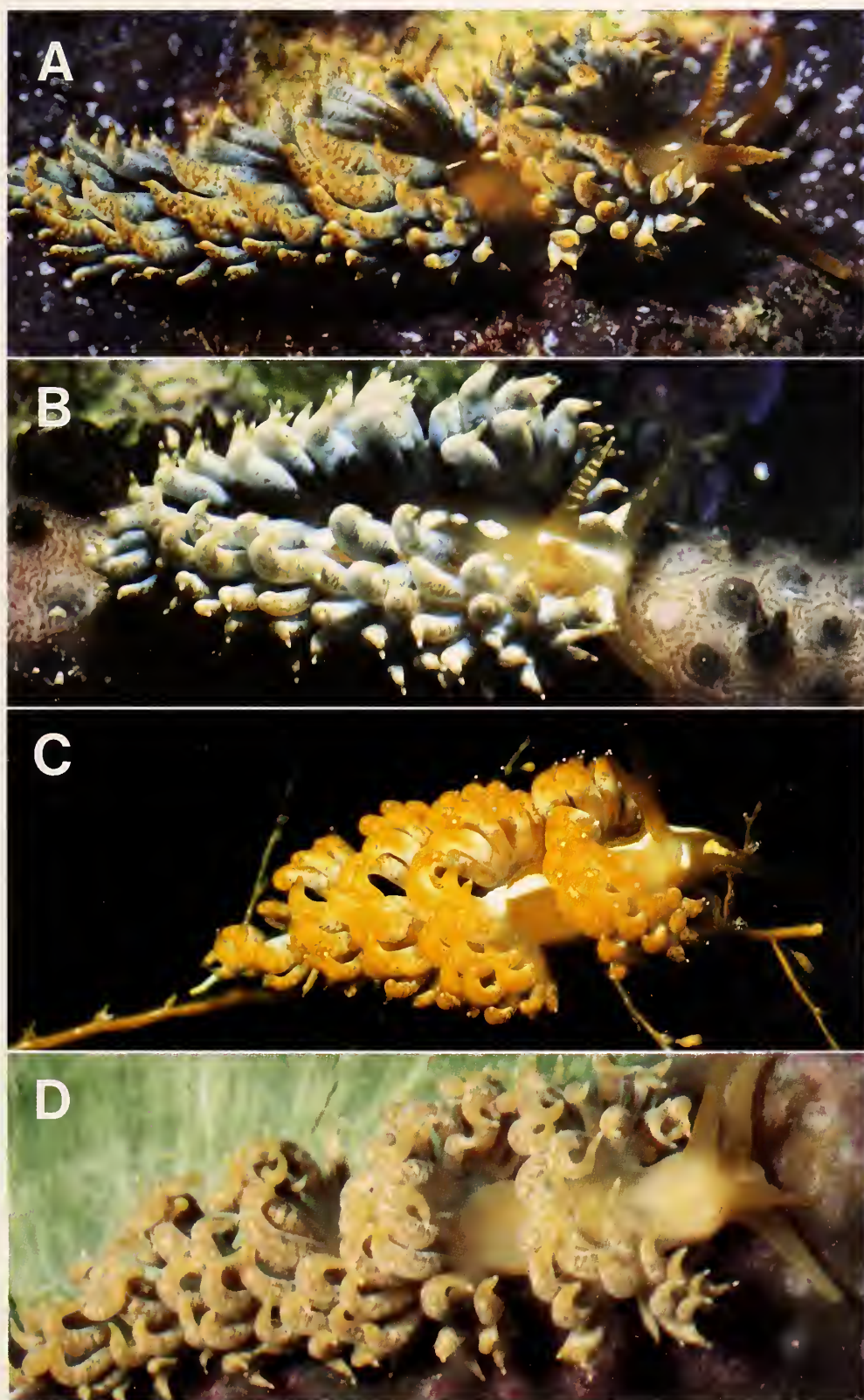
rhinophores. Live specimens measured up to 46 mm in length. The evenly tapered oral tentacles are slightly flattened. They are held anterolaterally and have a dorsal white line, wider near the base. The rhinophores are weakly lamellate with sloping bars of spicules overlaid with white pigment (Figure 1A, B) or smooth (Figure 1C, D). They are slender and evenly tapered to a fine tip. The rhinophores are much smaller in diameter and one-half the length of the oral tentacles. They end with a minute white tip. The head is rounded; the mouth a vertical slit (Figure 2). The foot has propodial tentacles that recurve inwardly and may be frosted with white coloration dorsally. The anterior margin of the foot and the propodial tentacles are bilabiate, with a well-developed groove that is wider medially. The foot is slender, with a central groove and a conspicuous flange that is one-third wider than the body itself. The long, slender tail has a slight medial keel.

The cerata arise from raised, arched cushions. There are up to eight clearly differentiated clusters of cerata per side (Figure 3). The pre-cardiac arches have a double row of cerata with alternating insertions and more cerata in the anteriormost limbs. The post-cardiac clusters are all in the form of arches with one row of cerata, except for the anterior limb of the first post-cardiac arch which has a double row. Within each arch, the cerata increase in size towards the center. The cerata are curved towards the midline of the body and are up to 6 mm in length in preserved specimens. When disturbed, the animal curls the cerata tips forward in a defensive posture (Figure 4). Each cerata is oblong in cross section and attached on its inner side. The translucent cerata are suffused with the food-derived color. There are small, opaque white tips on the cnidosacs followed by a translucent band through which the long cnidosacs can be seen. The distal one-third of each cerata has opaque white or bluish white spots on an orange ground. On most specimens, the middle one-third has a mottled white or bluish white band, which is more prominent on the anterior face of each cerata, on a background color that varies according to the food. The proximal one-third of each cerata lacks opaque white spots and shows the color of the digestive gland. The ceratal branches of the digestive gland are nodular. In each cerata a central branch with rounded lobules extends to the ceratal walls. These lobes are alveolar-like and have a honeycombed appearance. The cerata surfaces are smooth, but appear pustulate because numerous white pigment spots are located on the lobes. The long, functional cnidosac is lined with large glandular cells. The cerata are easily autotomized and move about for a short time after detachment.

The genital apertures are located below the anterior

Figure 1

Color variation in *Pauleo jubatus* gen. & sp. nov., Millen & Hamann. A. 32 mm specimen, Discovery Bay, Jamaica. B. 26 mm specimen, Discovery Bay, Jamaica. C. 30 mm specimen, Grand Bahama, Bahamas. D. 42 mm specimen on prey, *Plexaurella dichotoma*, Guanaja, Honduras.



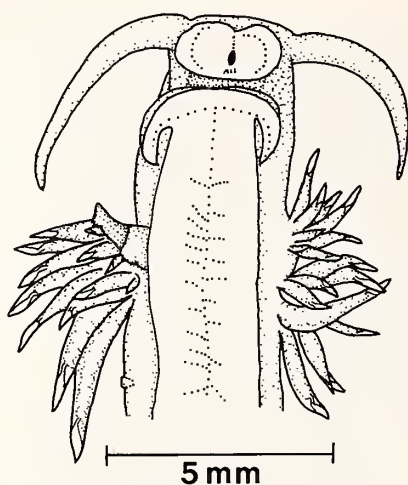


Figure 2

Pauleo jubatus, ventral view of head and foot.

limb of the first ceratal arch; the anal opening is posterior, within the second arch; and the renal pore is located in front of the second arch, in the interhepatic space (Figure 3).

Digestive system: The buccal mass has a circular, muscular, lip plate. The portion surrounding the mouth slit is convoluted and chitinized. The jaws (Figure 5) are covered by thin, unpigmented epithelium. They are pale golden brown in color, and rectangular, with a vertical flange for muscle attachment, and more posteriorly, a concave dorsal margin. The wing of each jaw is divided by a slight groove into an upper and a lower portion. The upper portion is smaller, lighter in color, and more convex than the lower portion (Figure 5A). The small masticatory process bears, near its tip, one row of approximately 10–18 small denticulations (Figure 5B).

The radular formula is 20–23 (0·1·0). The teeth have an elongate, bluntly pointed cusp with 9–14 small denticles on each steeply sloping side. A long pair of posterior limbs forms a narrow arch (Figure 6A). In some animals, in-

termediate denticles are present (Figure 7). In lateral view (Figure 6B), a prominent knob for articulation projects outward. The teeth are large: 200–460 μm long and 77–240 μm wide.

Oral glands are absent, and the small salivary glands are located dorsolaterally above the anterior portion of the stomach with long ducts inserting on the buccal bulb just above the buccal ganglia. The short, wide oesophagus is lined with cuticle on the dorsal and lateral sides.

The S-shaped stomach has three parts. The forward portion is an elongate oval, curved slightly to the left, with longitudinal papillate striae. The smaller central portion arises dorsally and loops abruptly to the right through 90°, so its longitudinal striae are oriented transversely relative to the animal as a whole. Two anterior and one posterior hepatic ducts branch off this portion. The posterior portion of the stomach loops ventrally and to the left, narrowing gradually into the intestine. The latter runs longitudinally under the posterior hepatic duct and then abruptly bends dorsally and to the right to empty within the second ceratal arch. Each ceratal arch is served by one branch of the digestive gland.

Central nervous system: The oval cerebropleural ganglia are completely fused and connected together by a short wide commissure. The rhinophoral ganglia are on long stalks. The eyes are on very short stalks. Small statocysts lie behind the optic ganglia. The oval pedal ganglia are joined to the larger cerebropleural ganglia by short commissures, and to each other by a longer, wide, circumoesophageal commissure. The oval buccal ganglia lie beneath the oesophagus and are attached to each other by a short commissure.

Reproductive system (Figure 8): The ovotestis form large, round, grape-like lobules with the female ancini peripheral to the male ancini. There is a long thin ovotestis duct. The duct widens into a sausage-shaped hermaphroditic ampulla, which coils twice and then extends the length of the female gland mass, narrowing only slightly before bifurcating into a narrow oviduct and a wide vas deferens. The vas deferens is highly muscular until it enters the penis. The vas deferens does not have a distinct prostatic portion,

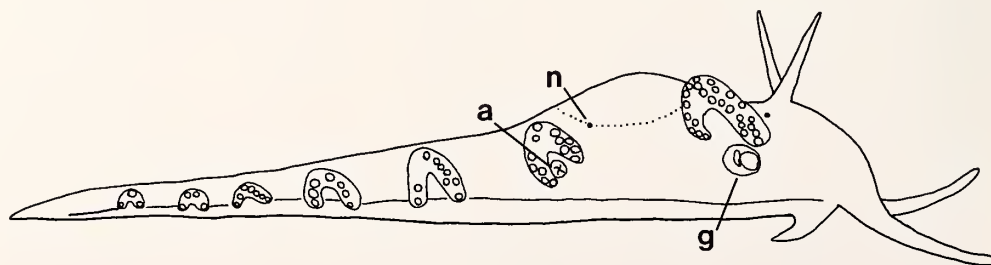


Figure 3

Right lateral view of *Pauleo jubatus* showing position of ceratal insertions. Key: a, anus; n, nephroproct; g, genital apertures.



Figure 4

Pauleo jubatus showing defensive bristling of the cerata with the cnidosacs pointing anteriorly.

although it is lined with a single layer of ciliated cuboidal cells, which are probably secretory in function. It loops and then enters a fibrous penial sac, which becomes wrinkled and deflated looking when the penis is everted. When the penis is withdrawn, the sac envelops the entire vas

deferens and upper portion of the penis. Inside the non-glandular penial sac, the muscular vas deferens enters the proximal portion of the penis. The penis is large, elongate, and flattened in cross section. In preserved specimens it is usually everted, with a small, slightly papillate sheath at its base. The vas deferens opens subterminally and the flattened tip is asymmetrical. The penis has highly muscular walls and an internal network of transverse muscle fibres, lacunae, and peripheral glandular cells which are larger on the posterior edge. The glandular cells become more numerous distally and occupy the entire tip of the penis beyond the opening of the vas deferens. No independent glandular opening was located and no internal duct entered the vas deferens.

There is a common atrium for the female gland mass and the vagina ventral to the posterior portion of the male aperture. The vagina forms the anterior face of the common

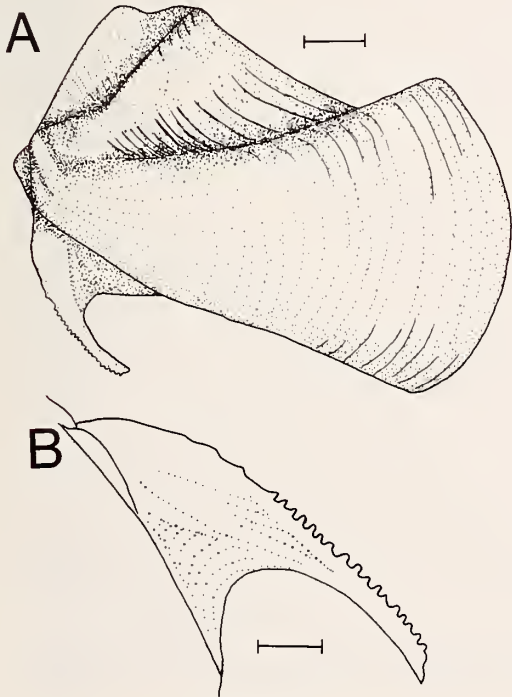


Figure 5

A. Outer view of right jaw plate of *Pauleo jubatus*. Scale bar = 0.1 mm. B. Masticatory margin of jaw plate showing denticles. Scale bar = 100 μ m.

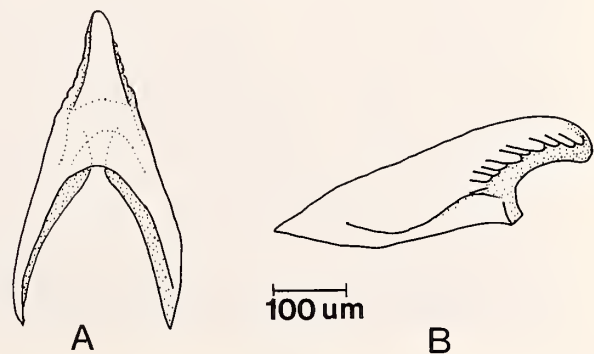


Figure 6

A. Dorsal view of a radular tooth of *Pauleo jubatus*. B. Lateral view of a worn radular tooth showing denticles.

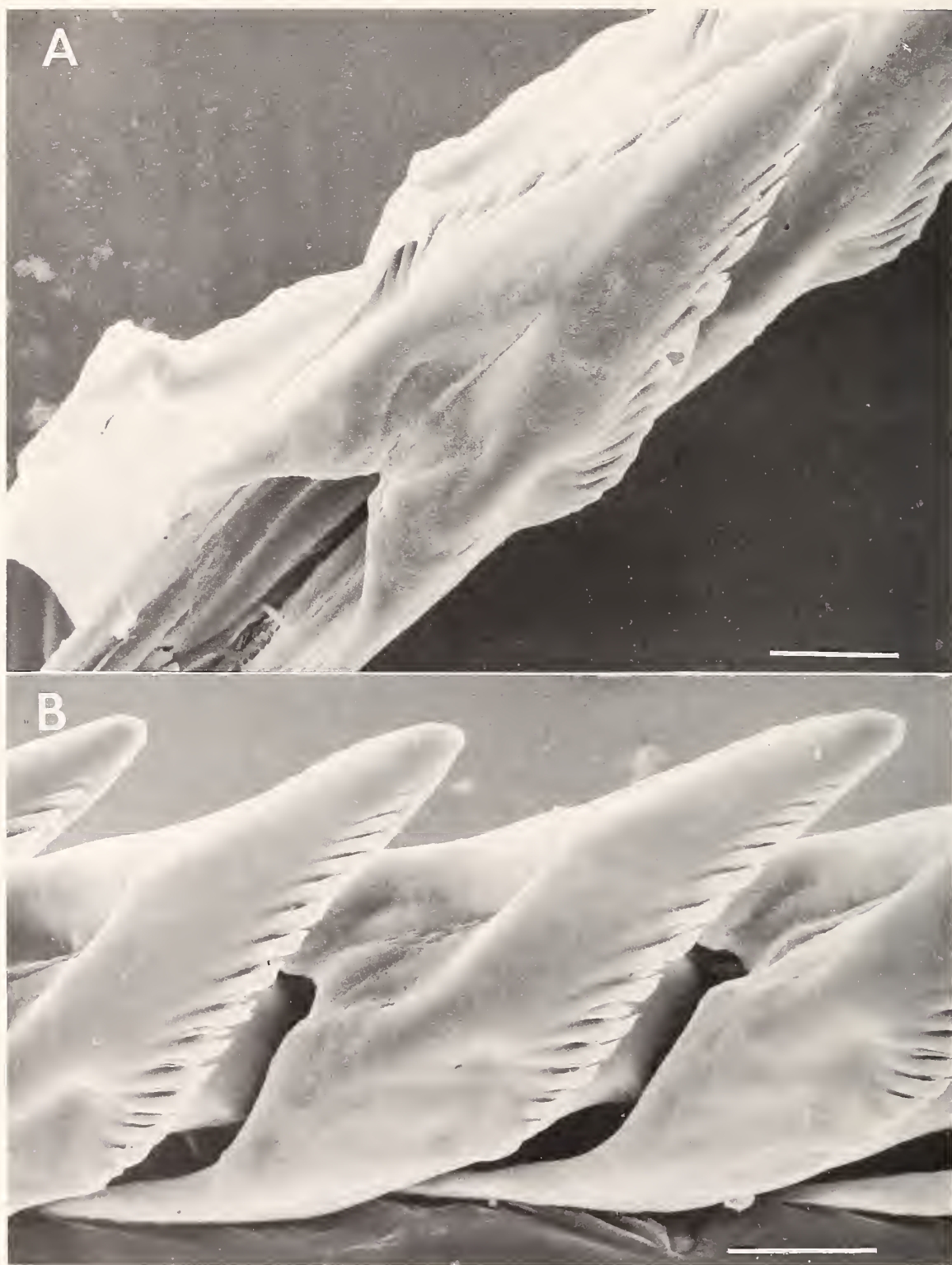


Figure 7

A. SEM view of the dorsal surface of an unused radular tooth of *Pauleo jubatus*. B. Dorsolateral view showing presence of intermediate denticles. Scale bar = 40 μ m.

duct and continues as a tubular oviduct to the junction with the seminal receptacle. The semiseriably arranged receptacle is elongate and irregularly lobate, with a short stalk. The long, tubular oviduct joins the hermaphroditic duct. The female gland mass is composed of a highly convoluted membrane gland, a small albumen gland, and a large mucous gland. The latter consists of two distinct lobes with the genital organs running down the groove between them.

Ecology: Little is known about this species. All specimens have been collected or photographed at night. They are usually found on the side of coral heads, on sandy bottoms, in 8–20 m of water. The darkest specimens, with a bluish gray cast to the body and dark blue-gray ceratal cores, were found feeding on the gorgonian *Plexaurella dichotoma*, as were some pale pinkish-tan specimens (Figure 1B, D). Functional nematocysts are present in the cnidosacs. The animal varies in color, which probably comes from a varied diet. Most dissected specimens had empty stomachs or fragments of soft polyps, but one specimen was full of opisthobranch eggs, suggesting that they are opportunistic feeders. Their spawn mass has not been seen.

DISCUSSION

Pauleo jubatus can be distinguished from all other aeolids in the Caribbean by its large body size and the defensive bristling of its cerata. *Phidiana lynceus*, which is not as large, has some orange coloration, but it can be easily distinguished because the cerata are in rows and have one or two white bands on each ceras.

The taxonomy of the aeolid family Facelinidae has recently undergone a number of rearrangements, summarized by EDMUNDS & JUST (1983) and WILLAN (1987). We favor their use of the family Facelinidae rather than the more all-encompassing Glaucidae proposed by MILLER (1974). The subfamily Favorininae is composed of genera whose cerata are arranged in arches, but this trait is considered polyphyletic so the subfamilies should probably be abandoned (EDMUNDS, 1970; WILLAN, 1987; GOSLINER, 1991). Generic placements are also rather unsatisfactory at present because most genera are separated almost entirely on the basis of different penial structures. These differences have been reviewed by MILLER (1974). Since then, however, three new genera have been added, *Hermosita* and *Bajaeolis* by GOSLINER & BEHRENS (1986) and *Anetarca* by GOSLINER (1991).

This new genus *Pauleo* has both pre- and post-cardiac ceratal clusters arranged in arches on elevated cushions, some of which bear double rows of cerata. A number of genera have the synapomorphy of cerata in arches rather than rows, which is the basis of the polyphyletic subfamily Favorininae. Raised ceratal cushions appear to be a derived state because none of the plesiomorphic reproductive characteristics (two bursae, serial receptaculum seminis) occur in these genera. This parallels the situation in the family

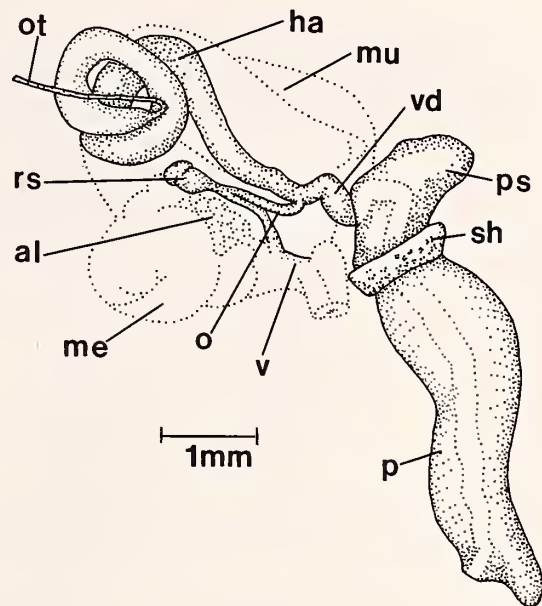


Figure 8

Reproductive system of *Pauleo jubatus* drawn using a camera lucida. Key: al, albumen gland; ha, hermaphroditic ampulla; me, membrane gland; mu, mucous gland; o, oviduct; ot, ovotestis duct; p, penis; ps, penial sac; rs, receptaculum seminis; sh, sheath; v, vagina; vd, vas deferens.

Flabellinidae (GOSLINER & GRIFFITHS, 1981). Multiple insertions of cerata on the arches are a plesiomorphic feature. All of the genera with raised, arch-shaped cushions are compared in Table 1, except for *Amanda*, *Godiva*, *Noumeaella*, and *Echinopssole*, which have apomorphic penial armature.

In addition to the arrangement of the cerata, other external features sometimes used for generic diagnosis are the shape of the rhinophores and the position of the genital openings. *Pauleo jubatus* has smooth or lamellate rhinophores and reproductive openings at the anterior limb of the first ceratal arch. These are both apomorphic conditions for the family (WILLAN, 1987) but because they occur in a number of genera in both subfamilies, they are not very helpful for comparative purposes.

Internally, the jaw structure of *Pauleo jubatus* has a number of apomorphies. It has an indented dorsal margin, a dorsal flange, and an upper and lower convex division separated by a groove. Each of these traits can be found in other genera from both subfamilies in the Facelinidae. However, only the genera *Dondice* Marcus, 1958, *Facalana* Bergh, 1888, and *Sakuraeolis* Baba & Hamatani, 1965, and the species "*Godiva*" *banyluensis* Portmann & Sandmeier, 1960, share all three apomorphies (Table 1). Their jaws all show an intermediate modification towards the extreme type found in the Glaucidae. The jaws of *Pauleo jubatus* are more elongate than all of the others, and differ from those of *Sakuraeolis* by having only one row of den-

Table 1

Genera of Favorininae having multiple rows of cerata on raised arch-shaped pedicles, and having no penial armature.

Genus	Rhinophores	Jaw		Masticatory border rows	Vas deferens	Penis
		Notch	Flange			
<i>Austraeolis</i>	annulate	—	+ (—)	single	proximal prostatic	circle of fleshy filaments
<i>Bajaeolis</i>	perfoliate	+	—	several	all prostatic	conical
<i>Dondice</i>	annulate	+	+	single	non-prostatic	basal gland, spiral groove, prostate gland
<i>Facalana</i>	perfoliate	+	+	single	?	leaflike expansion, fleshy glandular knobs
<i>Jason</i>	papillate	—	—	smooth	all prostatic	distal glands
<i>Pauleo</i>	smooth or perfoliate	+	+	single	non-prostatic	basal sac, internal glands
<i>Sakuraeolis</i>	smooth	+	+	several	all prostatic; 1 cell layer thick	fleshy lobes, stalked accessory gland
" <i>Godiva</i> " <i>banyluensis</i>	perfoliate	+	+	single	proximal prostatic	basal sac, conical penis

ticles and from those of "*Godiva*" *banyluensis* by lacking a flange-like guard.

Variations of the basic facelinid radula may be adaptations to different prey. The steep-sloping sides and many fine denticles on the radula of *Pauleo jubatus* are characteristic of the genus *Phyllodesmium* Ehrenberg, 1831. *Pauleo jubatus* was not placed in the genus *Phyllodesmium* because it has functional cnidosacs, the cerata are in arches on raised pads, and the large penis is highly muscular with internal glands. Most species of *Phyllodesmium* feed on alcyonacean octocorals and have symbiotic zooxanthellae, but *P. horridum* (Macnae, 1954) and *P. serratum* (Baba, 1949) feed on gorgonaceans (GOSLINER, 1987; RUDMAN, 1991).

Phyllodesmium horridum has teeth that are almost identical in shape to those of *Pauleo jubatus*, although they are proportionally much smaller—about one-half the size in similar sized animals. Externally, *Phyllodesmium horridum* differs from *Pauleo jubatus* due to its wider, more depressed shape, longer cerata, which are not borne on raised pads, and less tapering ceratal tips, rhinophores, and oral tentacles. Internally, the jaw of *Phyllodesmium horridum* is not as elongate, and its masticatory denticles are less developed. Both have a two-part jaw with a flange, but in *Phyllodesmium horridum* the two parts are not separated by a large notch and the smaller flange extends horizontally rather than vertically. The penial structures of the two species also differ greatly. *Phyllodesmium serratum* has a thin-walled, prostatic vas deferens, which terminates in a very tiny, muscular penis tip. The vas deferens of *Pauleo jubatus* is shorter, narrower, and muscular with a large, muscular penis containing internal glands.

Penial elaborations distinguish the various genera of Facelinidae. Table 1 compares species of the subfamily Favorininae that are most similar in ceratal arrangement to *Pauleo* and that do not have penial armature. The non-

glandular penial sac of *Pauleo* is found only in the species "*Godiva*" *banyluensis* (PORTMANN & SANDMEIER, 1960). This thoroughly described species has recently been removed from the genus *Godiva* because it lacks a penial spine (WILLAN, 1987). Previously it was removed from the original genus *Dondice* because it lacks a separate prostate in the penis and a basal penial gland (EDMUNDS, 1964). It is presently without a generic assignment. Although the sac around the vas deferens is like that in *Pauleo*, the rest of the male reproductive system is radically different. "*Godiva*" *banyluensis* has a long vas deferens that is prostatic before it enters the sac, but not after. Its conical penis does not contain internal glands. On the other hand, the elaborate stomach of this species, described by GARCÍA & GARCÍA (1984), resembles that of *Pauleo jubatus*.

Similar penial glands to those of *Pauleo jubatus* are found in the genera *Dondice*, *Jason*, and *Sakuraeolis*. *Jason* is separated on the basis of unusual jaw and radular morphology (MILLER, 1974) but *Dondice* and *Sakuraeolis* appear to be closely allied to *Pauleo*. The penises of both of these latter species are large, with interlacing musculature, blood lacunae, and internal glands. *Dondice occidentalis* (Engel, 1925) has an accessory penial gland at the base of the penis with a duct extending distally and emptying into the vas deferens either near the penis tip (MARCUS, 1958) or part way along the penis (EDMUNDS, 1964). It also has a prostate gland located inside the penis, which opens independently at its tip. This latter gland is similar to the penial gland found in *Pauleo*, although no separate duct could be found in histological sections. *Pauleo* lacks the basal penial gland of *Dondice*, although it has a non-glandular sac in the same position.

Sakuraeolis has a stalked accessory gland similar to the unstalked gland of *Dondice*. It does not have a separate prostate gland inside the penis, but the vas deferens is reported to be prostatic throughout its length, even though

it consists of only a single cell layer (BABA & HAMATANI, 1965). It appears that the vas deferens of *Pauleo* is similar. The penis of *Sakuraeolis* has fleshy flaps at the base of the penial gland, which are not found in either *Pauleo* or *Dondice*. The genital openings of both *Sakuraeolis* and *Dondice* are more posterior than those of *Pauleo*, and their teeth are different.

In conclusion, although *Pauleo* is clearly allied to a number of genera in the Favorininae, it possesses a unique combination of characteristics that do not comfortably fit into any other generic diagnosis. The newly created genus *Pauleo* presently contains only the type species, *Pauleo jubatus*.

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